



Ecological niches and potential geographical distributions of Mediterranean fruit fly (*Ceratitis capitata*) and Natal fruit fly (*Ceratitis rosa*)

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ABSTRACT

Aim To predict and compare potential geographical distributions of the Mediterranean fruit fly (*Ceratitis capitata*) and Natal fruit fly (*Ceratitis rosa*).

Location Africa, southern Europe, and worldwide.

Methods Two correlative ecological niche modelling techniques, genetic algorithm for rule-set prediction (GARP) and a technique based on principal components analysis (PCA), were used to predict distributions of the two fly species using distribution records and a set of environmental predictor variables.

Results The two species appear to have broadly similar potential ranges in Africa and southern Europe, with much of sub-Saharan Africa and Madagascar predicted as highly suitable. The drier regions of Africa (central and western regions of southern Africa and Sahelian zone) were identified as being less suitable for *C. rosa* than for *C. capitata*. Overall, the proportion of the region predicted to be highly suitable is larger for *C. capitata* than for *C. rosa* under both techniques, suggesting that *C. capitata* may be tolerant of a wider range of climatic conditions than *C. rosa*. Worldwide, tropical and subtropical regions are highlighted as highly suitable for both species. Differences in overlap of predictions from the two models for these species were observed. An evaluation using independent records from the adventive range for *C. capitata* and comparison with other predictions suggest that GARP models offer more accurate predictions than PCA models.

Main conclusions This study suggests that these species have broadly similar potential distributions worldwide (based on climate), although the potential distribution appears to be broader for *C. capitata* than for *C. rosa*. *Ceratitis capitata* has become invasive throughout the world, whereas *C. rosa* has not, despite both species having broadly similar potential distributions. Further research into the biology of these species and their ability to overcome barriers is necessary to explain this difference, and to better understand invasion risk.

Keywords

Ceratitis capitata, *Ceratitis rosa*, ecological niche models, fruit flies, GARP, PCA, potential distribution.

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INTRODUCTION

Fruit flies (Diptera: Tephritidae) are globally distributed picture-winged flies of variable size. Tephritidae, with > 4000 species described, ranks among the most diverse groups of true flies (White & Elson-Harris, 1992; Thompson, 1999). They are almost all phytophagous, with larvae developing in the seed-

bearing organs of plants. Although they are commonly named 'fruit flies', larval development can take place in other parts of host plants as well as fruits, including flowers and stems. About 35% of fruit fly species attack soft fruits, including many commercially important ones (White & Elson-Harris, 1992).

Several representatives of this family are of critical importance as pests of fruit crops (Thompson, 1999). Economic

impacts can be enormous, and costs of control or eradication can require substantial budgets. For example, Dowell & Wange (1986) stated that establishment of major fruit fly threats to the Californian fruit industry would cause crop losses of US\$910m yearly, and an eradication program a cost of US\$290m. The recent (1999) eradication of the papaya fruit fly (*Bactrocera papayae* Drew & Hancock) from Northern Queensland in Australia cost AUS\$34m (<http://www2.dpi.qld.gov.au/health/4665.htm>). Annual losses in revenue in the eastern Mediterranean (Israel, Palestinian Territories, Jordan) linked to fruit fly infestations are estimated at US\$192m (Enkerlin & Mumford, 1997); in Egypt, annual losses due to the introduced peach fruit fly, *Bactrocera zonata* (Saunders), are estimated at €190m (http://www.eppo.org/QUARANTINE/insects/Bactrocera_zonata/DSDACUZO.pdf). Most economically important fruit fly pests belong to four genera: *Anastrepha* Schiner (New World Tropics), *Bactrocera* Macquart, *Ceratitidis* MacLeay and *Dacus* Fabricius (Old World Tropics).

In the African tropics, *Ceratitidis* flies cause most of the damage to soft fruits of economic value. This genus comprises > 90 species, all native to the Afrotropical region (De Meyer, 2001). The genus includes both polyphagous species with wide host ranges, and stenophagous clades of species specialized on particular host plant genera (De Meyer *et al.*, 2002; De Meyer, 2005). The medfly, *Ceratitidis capitata* (Wiedemann), is the most widespread and probably the most serious pest species in the family (White & Elson-Harris, 1992). It was originally restricted to the tropics of mainland Africa, but has readily colonized tropical and mild temperate habitats far outside its home range, and now occurs on five continents (Gilstrap & Hart, 1987).

The medfly is not unique in its invasive potential. Several other fruit flies have been introduced accidentally into countries with established fruit industries in spite of quarantine procedures (see examples above; reviewed by Duyck *et al.*, 2004). Specifically, within *Ceratitidis*, other polyphagous species appear to have potential for introductions similar to the medfly; of particular interest, the Natal fruit fly, *Ceratitidis rosa* Karsch, is a polyphagous species with a wide range on the African mainland (De Meyer, 2001) that has invaded some Indian Ocean islands (White *et al.*, 2001), where it displaced the introduced medfly (Duyck *et al.*, 2004). Some studies also indicate that *C. rosa* might be more tolerant of colder and wetter conditions than the medfly (Normand *et al.*, 2000; Duyck *et al.*, 2004, 2006), suggesting greater potential for establishment in temperate regions.

The purpose of this study is to compare potential geographical distributions of *C. capitata* and *C. rosa*, both in the Afrotropics and worldwide. Comparisons are based on ecological niche requirements (largely in climatic dimensions) modelled based on their ecological distributions in their regions of origin (these models are referred to here as ecological niche models). Models of invasive potential are developed and tested quantitatively for *C. capitata* as a measure of the predictive power of the methodology, then applied to *C. rosa*, which is not broadly invasive in continental regions outside Africa.

MATERIAL AND METHODS

Occurrence data

Native-range distributional data for *C. capitata* and *C. rosa* were derived from relational data bases housed at the Royal Museum for Central Africa, and maintained by the first author (<http://projects.bebif.be/enbi/fruitfly>). The data base contains Afrotropical specimen data for the ceratitidine (Tephritidae, Dacinae, tribe Ceratitidini) fruit fly genera *Ceratitidis*, *Trirhithrum* Bezzi, and *Capparimyia* Bezzi, and summarizes the holdings of all major European, African and North American natural history collections, supplemented with a few records from specimens housed in the National Insect Collection at Pretoria, South Africa. Only records with authoritative confirmation of identification were included; those with doubtful identification were excluded from model building. In total, 265 and 246 records were available for *C. capitata* and *C. rosa*, respectively. Records for *C. rosa* do not include the former variety *fasciventris* (Bezzi) as this is now recognized as a separate species (De Meyer, 2001).

For *C. capitata*, we gathered information on non-native (outside Africa) populations globally, to enable quantitative tests of the predictive ability of the ecological niche models regarding observed occurrences in distant regions. Global occurrence localities were obtained from literature (Hooper & Drew, 1989; De Longo *et al.*, 2000; Smallridge & Hopkins, 2002; Petit-Mary *et al.*, 2004) and electronic resources (see Table S1 in Supplementary Material for a list of sources). The resulting data reflect both contemporary as well as historical records of medflies outside Africa, and permanent as well as temporary establishments. The list is clearly not exhaustive (it does not give a complete image of actual or historical distribution of medflies worldwide), but is sufficient to provide a test of model predictions. We used only records of permanent establishment for model testing.

Localities were georeferenced based either on coordinates provided directly on specimen labels for individual specimens, or on coordinates extracted from official gazetteers (e.g. GeoNet, <http://gnswww.nga.mil/geonames/GNS/index.jsp>) or from specialized locality data bases present in some of the natural history institutions, based on their collections. Records with unspecified or unknown localities were removed from consideration; the remaining records were then plotted on maps and inspected visually to detect obvious errors; records considered questionable along margins of distributions were investigated individually. In cases where multiple records were available for a particular locality, only one was used in analyses.

Only occurrence data originating from the original (native) distributions of each species were used to generate model predictions. For *C. rosa*, we used as the native range the entire African mainland, exclusive of the Indian Ocean Islands; for *C. capitata*, we assumed a native range in southern to eastern Africa; these decisions are based on a recent review (De Meyer *et al.*, 2004) and are supported by other studies (Baliraine *et al.*, 2004; but cf. Gasparich *et al.*, 1997). In practice, all

records coinciding with the phytochoria Cape, Eastern Zambezi, Zanzibar–Inhambane and Tongaland–Pondoland (White, 1984) were considered to constitute the original distribution of *C. capitata*.

Environmental data

Data sets used to characterize environments across Africa and worldwide consisted of interpolated 'bioclimatic' variables (2.5' spatial resolution, derived by the WorldClim project, <http://biogeo.berkeley.edu>). Procedures followed in producing these interpolated climate surfaces are described by Hijmans *et al.* (2005). The particular variables used in the genetic algorithm for rule-set prediction (GARP) and principal components analysis (PCA) (Table 1) were chosen to represent environmental dimensions maximally relevant to ecological distributions of small arthropods. No vegetation-cover layers were used, given the heterogeneous nature of habitats (including man-made horticultural environments) that can potentially be occupied by the target taxa because of their polyphagous host range.

The quality of the interpolated climate surfaces is influenced by the density of weather stations: they are least reliable where density is low (Hijmans *et al.*, 2005). In parts of Africa the density is low, particularly in the drier regions such as the Sahara and Kalahari (Hijmans *et al.*, 2005). Botswana, in particular, has very few stations. However, regions of southern and eastern Africa that correspond with the distribution records for the two flies have a high density of weather stations. The areas around the Mediterranean basin, most of Europe and North America also have a high density of weather stations. For maps indicating the density of weather stations used in interpolating the climate surfaces see Hijmans *et al.* (2005).

Ecological niche modelling

Our approach is based on the idea of modelling species' ecological niches, which have been shown to constitute long-term stable constraints on species' potential geographical distributions (Peterson *et al.*, 1999; Peterson, 2003; Raxworthy *et al.*, 2003; Martínez-Meyer *et al.*, 2004; Wiens & Graham, 2005). Ecological niches are defined here as the set of

conditions under which a species is able to maintain populations without immigration (Grinnell, 1917, 1924). Several avenues of research have demonstrated accurate predictions of invasive species' potential distributions (Peterson & Viegals, 2001; Welk *et al.*, 2002; Peterson, 2003; Peterson & Robins, 2003; Peterson *et al.*, 2003a,b; Morrison *et al.*, 2004; Thuiller *et al.*, 2005). Our approach consisted of three steps: (1) model ecological niche requirements of species based on known occurrences on native distribution areas; (2) test accuracy of native-range predictions based on subsets of available data; and (3) project niche model globally to identify areas putatively susceptible to invasion.

Two correlative ecological niche modelling techniques were used to predict distributions of the two fly species – the genetic algorithm for rule-set prediction (GARP, Stockwell & Noble, 1992; Stockwell, 1999; Stockwell & Peters, 1999) and a principal components analysis (PCA)-based modelling technique (Caithness, 1995; Robertson *et al.*, 2001).

Spatial predictions of presence and absence can include two types of error: omission (predicted absence in areas of actual presence) and commission (predicted presence in areas of actual absence; Fielding & Bell, 1997). Because GARP is a random-walk procedure, it does not produce unique solutions; consequently, we followed recently published best practice approaches to identify optimal subsets of resulting replicate models (Anderson *et al.*, 2003). In particular, for each species we developed 100 replicate models; of these models, we retained the 20 with lowest omission error. Then we retained the 10 models with intermediate commission error (we discarded the 10 models with area predicted present showing greatest deviations from the overall median area predicted present across all low-omission models). This best subset of models was summed to produce final predictions of potential distributions in the form of grids with values ranging from 0 (all models agree in predicting absence) to 10 (all models agree in predicting presence).

As the two modelling techniques (GARP and PCA) use different approaches, the maps produced from them do not follow the same suitability scales. The different ranges (probability values of PCA, prediction values in GARP) were grouped in three classes and represented by different shadings on the maps. In these maps, regions of 'high' suitability have the darkest shading and regions of 'low' suitability have the lightest shading. The suitability scales therefore represent relative suitability within each data set, but cannot be interpreted as equal absolute values that are directly comparable.

Model testing

To evaluate and test our model predictions, we compared their ability to predict independent sets of test points with that expected under null models of no association between test points (assumed independent of one another) and model prediction. Because our goal was predicting global invasive potential, we tested model predictivity only for *C. capitata*, the species with the broadest adventitious range, asking the

Table 1 Environmental data sets used in the development of ecological niche models.

Variable
Mean diurnal temperature range
Temperature seasonality (standard deviation \times 100)
Maximum temperature of warmest month
Minimum temperature of coldest month
Temperature annual range
Precipitation of wettest month
Precipitation of driest month
Precipitation seasonality (coefficient of variation)

question (statistically) whether the coincidence between prediction and test points was closer than would be expected by chance.

The most common mode of evaluating niche models or distribution models in recent literature is via the area under the curve in a receiver-operating characteristic (ROC) analysis (Elith *et al.*, 2006). However, ROC analysis is not appropriate to the present situation, for two reasons: (1) ROC requires absence data, which are not available in the present case; (2) ROC weights type 1 and type 2 errors equally, but the present conceptual basis for niche modelling (Soberón & Peterson, 2005) would weight omission error more heavily than commission error. Thus we judge ROC analyses inappropriate to the challenges faced here. Models were tested via binomial tests that incorporate dimensions of correct prediction of both presences (based on success in predicting independent test data) and absences (based on proportion of the area predicted present, which is taken as the probability of a success). Given our assumptions regarding native distributional areas of *C. capitata*, the universe of testing was taken as all continents except Antarctica, and exclusive of the native range in southern and eastern Africa. Models were tested at each threshold of model agreement in GARP, ranging from very narrow areas (all models agreeing) to broader areas (any model predicting), and in the PCA.

RESULTS

Figure 1 shows the distributional data available from Africa for *C. capitata* and *C. rosa*, respectively, after removal of doubtful and uncertain localities; for *C. capitata* data from the supposed native distributional area of the species are distinguished from non-native populations on the African continent. Countries from which the greatest numbers of records were available include South Africa, Zimbabwe, Tanzania and Kenya; only very few records were available from Mozambique. Records

were available for *C. rosa* from Malawi, although none was available for *C. capitata*. Records representing the non-native African range of *C. capitata* were scattered throughout west and central Africa.

The results of the GARP and PCA modelling on the African continent and southern Europe for *C. capitata* (Fig. 2) indicate overall similarity between the two algorithms: both predict most of sub-Saharan Africa and Madagascar as highly suitable for *C. capitata*. The PCA model shows a region of low suitability in the Democratic Republic of Congo that is not apparent from the GARP model. This area largely coincides with the heart of the Equatorial rain forest zone. PCA predicts higher suitability in large parts of the Horn of Africa, while GARP does not, except for the Ethiopian Highlands. The coastal regions of North Africa and the Mediterranean region are highlighted as suitable by both, although with differences. Larger areas of high suitability are predicted in southern Europe by GARP than by the PCA model, although the PCA model predicts high suitability in the regions around the Bay of Biscay (France, Spain) and the Gulf of Sirte (Libya), while GARP predicts lower suitability in the same regions.

We used adventive populations of *C. capitata* as a means of testing model predictivity in the challenge of broad extrapolation to identify suitable areas for the species globally. In both cases, model predictions were considerably better than expectations under random (null) models (binomial tests, both $P < 10^{-13}$), indicating that both approaches offer significant predictivity regarding the global potential distribution of the species. However, looking at the accumulation of predictive ability (avoidance of omission error) as a function of proportional area predicted present (see Fig. 6), it is clear that GARP models achieve high predictivity in smaller proportional areas, suggesting that GARP models offer more accurate predictions.

For *C. rosa*, both models predict much of sub-Saharan Africa and Madagascar as highly suitable (Fig. 3). In both,



Figure 1 Distribution records for *Ceratitis rosa* (crosses) and *C. capitata* (squares). Dotted squares indicate the native range of *C. capitata*; and open squares, non-native populations of *C. capitata*.

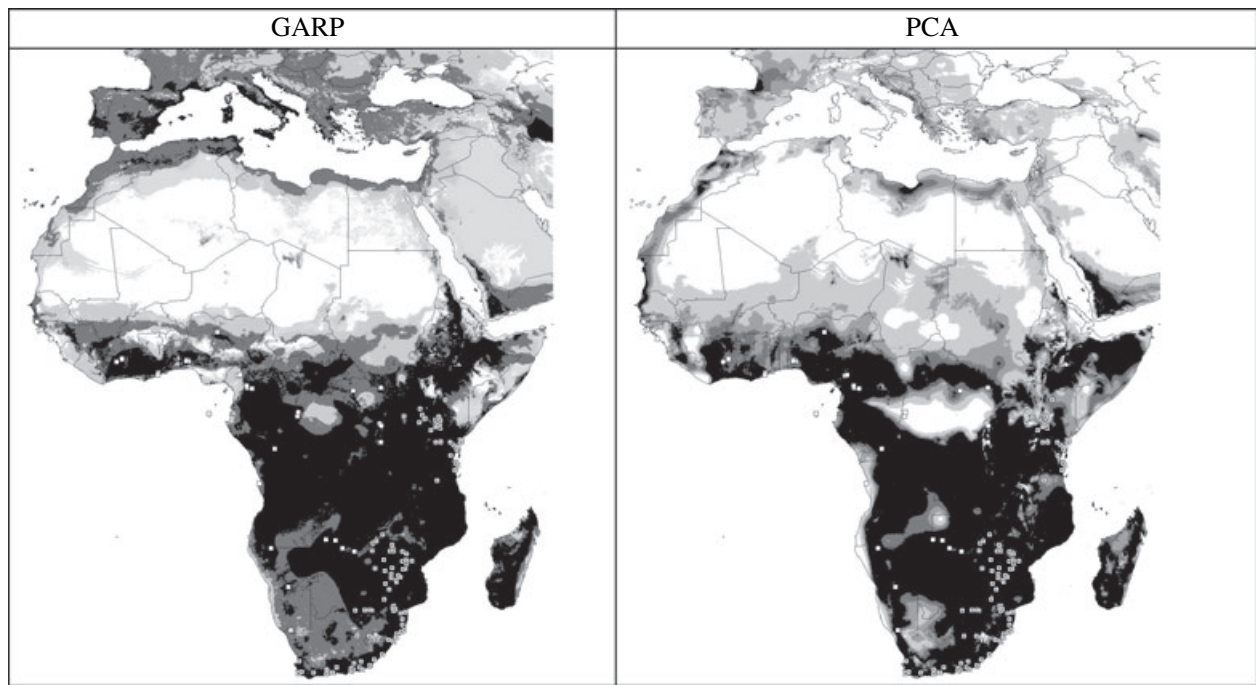


Figure 2 Predicted distribution of *Ceratitis capitata* in Africa and southern Europe, using a genetic algorithm for rule-set prediction (GARP) and a technique based on principal components analysis (PCA). White, predicted absence; light grey, low confidence in predicted presence; dark grey, higher confidence in predicted presence; black, high confidence in predicted presence. Dotted squares, native range; open squares, non-native populations of *C. capitata*.

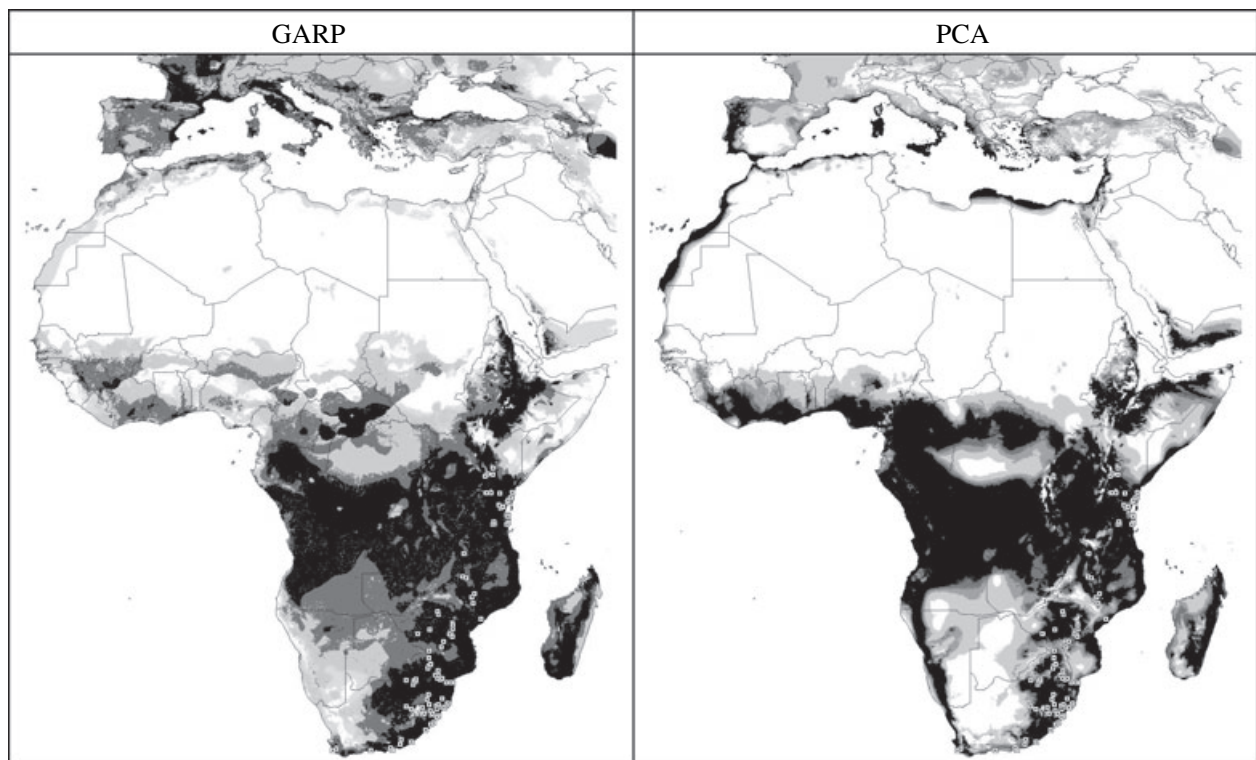


Figure 3 Predicted distribution of *Ceratitis rosa* in Africa and southern Europe, using a genetic algorithm for rule-set prediction (GARP) and a technique based on principal components analysis (PCA). White, predicted absence; light grey, low confidence in predicted presence; dark grey, higher confidence in predicted presence; black, high confidence in predicted presence.

parts of southern Europe also have high suitability values, but these regions do not overlap between the two models. A region of low suitability is evident for both in the drier central and western regions of southern Africa, as well as the Sahelian region. The PCA model has a narrow strip of high suitability along the northern and north-western coast of Africa, whereas these regions have much lower suitability values in the GARP predictions.

Projecting these models globally shows generally good agreement between the worldwide predictions and the non-native distribution records for *C. capitata* (Fig. 4).

Tropical and subtropical regions worldwide are, in general, highlighted as highly suitable for *C. capitata* (Fig. 4), but differences between the two models are evident. In North America, for example, regions of high suitability are considerably smaller in the PCA model than in the GARP model. In South America, a region of low suitability in southern Brazil and Uruguay in the PCA predictions is predicted at a much higher level in the GARP model. Regions of India and southern China are predicted to be suitable by both, but PCA identified generally smaller regions overall. In Australia, coastal regions only are identified as highly suitable in the PCA model, whereas broader regions in eastern and south-western Australia are found highly suitable in the GARP model.

For *C. rosa*, results were quite similar; tropical and subtropical regions worldwide are highlighted as highly suitable (Fig. 5). Differences between the two models exist for this species, and indeed agreement for this species appears to be lower than for *C. capitata* (Fig. 4). In North America, GARP highlights Florida and the eastern coastal region as being highly suitable, although this area is of lower suitability in the PCA model. Suitable areas extend to northern Argentina and Paraguay in the GARP model, but are of low suitability in the PCA model. Globally, the PCA model predicts smaller areas than the GARP model as being suitable (Fig. 6).

DISCUSSION

Evaluation of models

In addition to evaluating the predictions for *C. capitata* using distribution records from its adventive range, comparisons can be made with a prediction for this species that was made using the CLIMEX model (Vera *et al.*, 2002). The CLIMEX parameters used in the model were estimated using the geographical distribution in the Mediterranean region and using specific observations on overwintering survival (Vera *et al.*, 2002). They also made predictions that incorporated the impact of irrigation. When weekly rainfall was less than 25 mm, this was increased to 25 mm by using the appropriate option in CLIMEX (Vera *et al.*, 2002). Our predictions did not take the effect of irrigation into account.

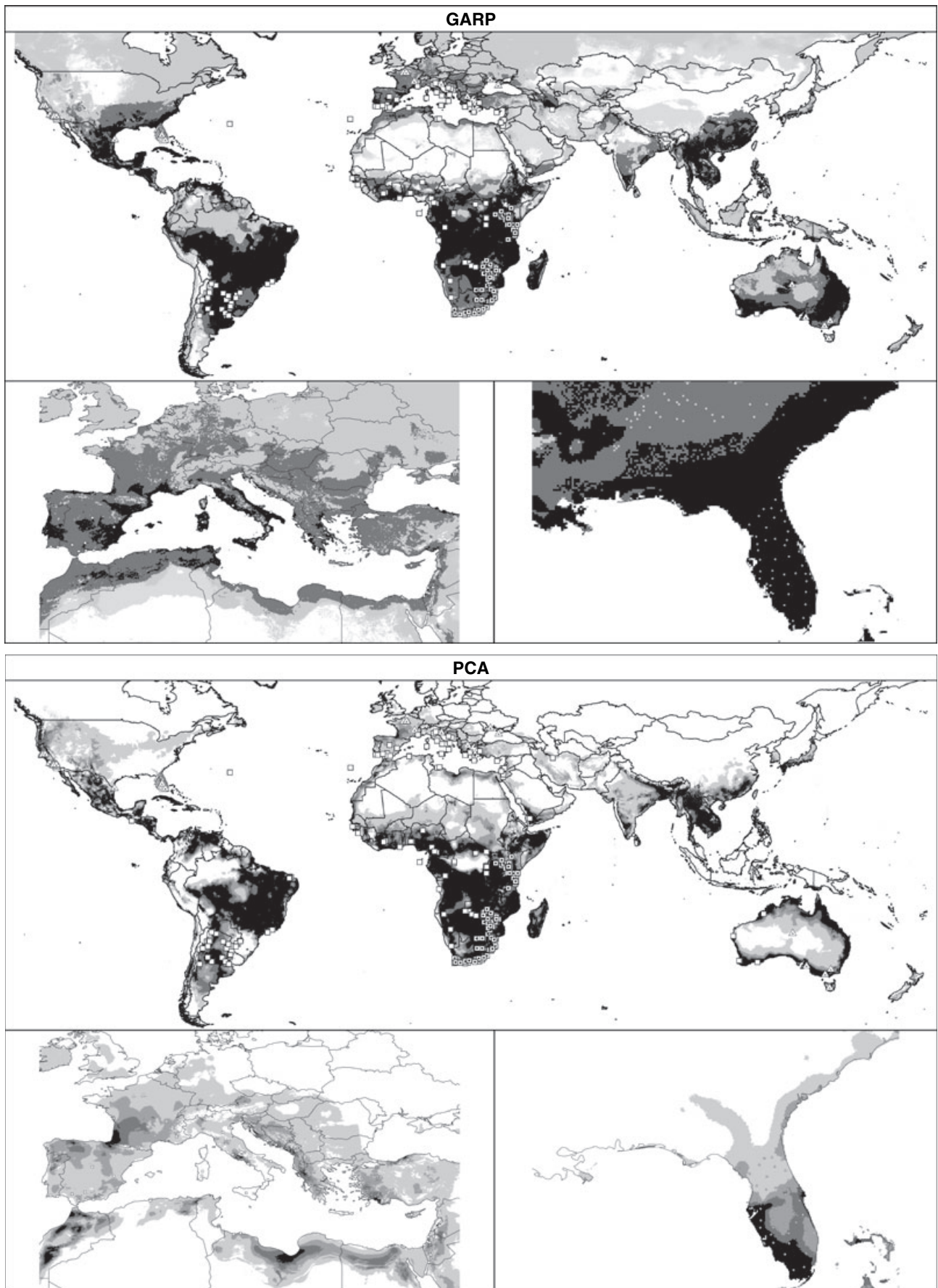
The worldwide predictions for *C. capitata* of Vera *et al.* (2002) using CLIMEX (without irrigation) appear to show a better match to the GARP prediction than to the PCA prediction. In particular, the match is closer in North America

and Australia. The regions of highest suitability predicted for *C. capitata* in southern Europe using the GARP model (Fig. 2) agree quite well with the CLIMEX prediction for the same region (Vera *et al.*, 2002). Most areas of highest suitability in the GARP prediction correspond with areas in the CLIMEX prediction with 'ecoclimatic index' values of 25 or above, locations that are considered very favourable for population growth and persistence. The PCA model (Fig. 2) showed less agreement with the prediction of Vera *et al.* (2002). The suitability values from the PCA model for southern Italy, Sicily and some of the Mediterranean islands are probably too low. An area of western France has a higher predicted suitability than regions around the Mediterranean, which is unexpected given the environmental conditions of the species' native range. It appears that the PCA model is not as good as the GARP model at capturing the species–environment relationship. This is probably because the PCA model cannot account for nonlinear species–environment relationships in the way that GARP can.

Comparing predictions between species

From the predictions, considerable overlap appears to exist in the potential distributions of these two species. They seem to have broadly similar potential ranges in Africa and southern Europe (Figs 2 & 3). An obvious difference in the predictions between the two species is the region of lower suitability in drier regions of Africa (central and western regions of southern Africa and Sahelian zone) for *C. rosa* compared with *C. capitata*, which is more pronounced in the PCA model than in the GARP prediction. A recent laboratory study by Duyck *et al.* (2006) found that *C. rosa* was more sensitive to low humidity than *C. capitata*; which would support this prediction. In addition, they found that *C. rosa* appeared to be better adapted to low temperatures than *C. capitata*, with a lower larval development threshold of 3.1°C compared with 10.2°C for *C. capitata* (Duyck & Quilici, 2002). However, it is not known to what extent these species co-exist in the wild throughout their native range. It is likely that each species dominates in particular regions of the climate space. Duyck *et al.* (2006) reported that *C. capitata* and *C. rosa* occupy different climatic niches on Réunion Island, where both species have been introduced. *Ceratitis capitata* dominates at temperatures of 24–26°C and rainfall of 0–1000 mm, whereas *C. rosa* dominates at temperatures of 22–23°C and rainfall of 3000–3500 mm (Duyck *et al.*, 2006). They predict that, given the climatic factors, niche segregation occurs between *C. capitata* and *C. rosa*, promoting co-existence between them (Duyck *et al.*, 2006). Caution is required as factors besides climatic ones can play a role. Different fruit preferences may also facilitate co-existence. The use of different host fruits has been shown to be important in reducing competition between the Oriental fruit fly *Bactrocera dorsalis* (Hendel) and *C. capitata* in Hawaii (Duyck *et al.*, 2004).

Regions around the Mediterranean basin had much higher suitability values for *C. rosa* than for *C. capitata* for the PCA



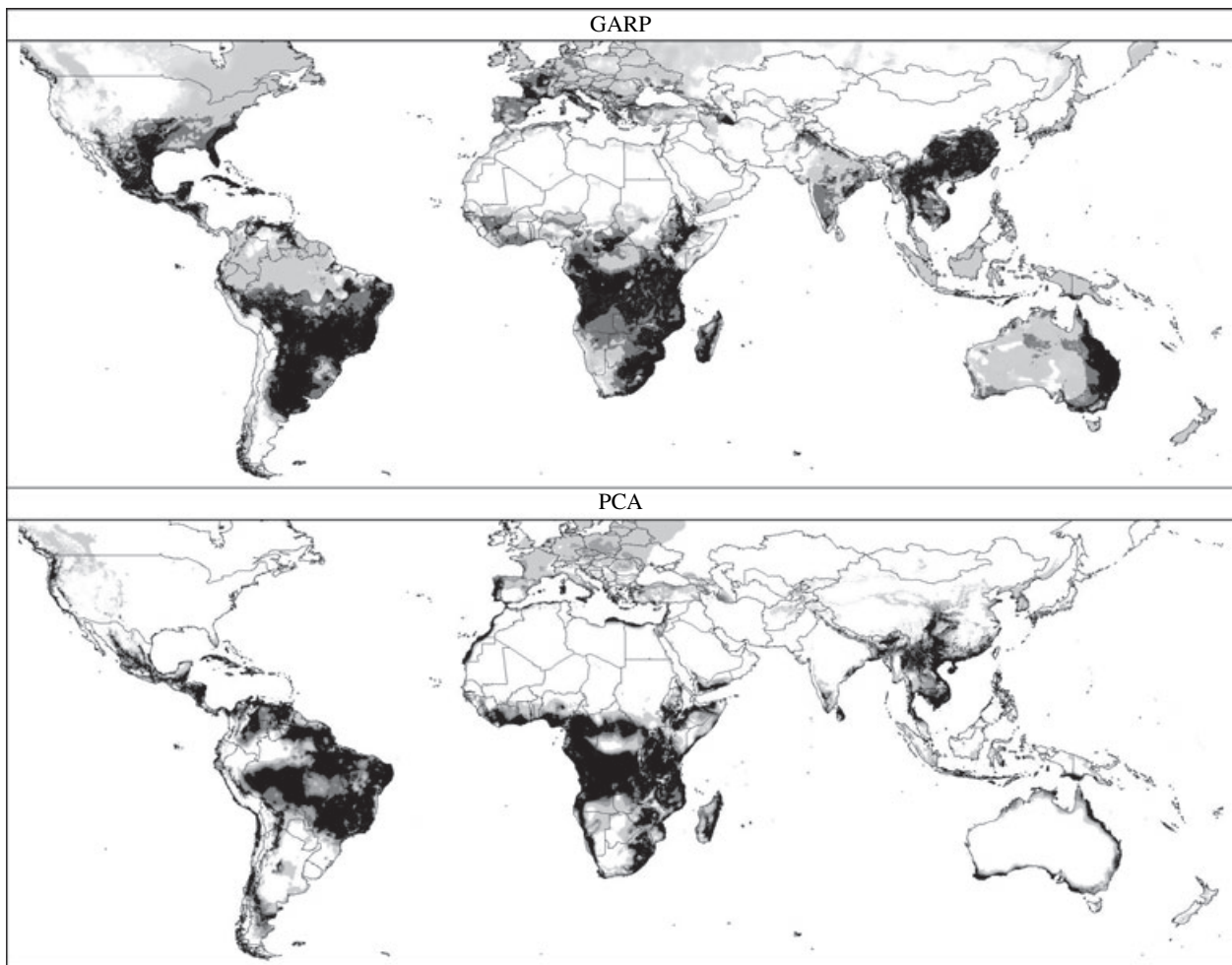


Figure 5 Predicted worldwide distribution of *Ceratitis rosa* using a genetic algorithm for rule-set prediction (GARP) and a technique based on principal components analysis (PCA). White, predicted absence; light grey, low confidence in predicted presence; dark grey, higher confidence in predicted presence; black, high confidence in predicted presence.

model, while GARP predicts higher suitability in some regions of Europe for *C. rosa* at higher latitude than for *C. capitata*. The overall proportion of the map region that is highly suitable for *C. capitata* is larger than that of *C. rosa*. This suggests that *C. capitata* may be tolerant of a wider range of climatic conditions than *C. rosa*.

Speculation on potential threat of *C. rosa* to other regions

Given the importance of *C. rosa* as a pest species, the risk of this species being introduced, establishing, and invading other regions of the world is of interest. Introduction into the area alone is insufficient to ensure that the species will

establish. For a species to become established in a new region, it has to overcome a number of barriers. The concept of barriers that restrict the spread of an introduced taxon in a region has a long history (Richardson *et al.*, 2000). An elegant explanation of the concept of barriers in invasion ecology is given by Richardson & van Wilgen (2004), which they used to explain plant invasions. Six barriers (A–F) were described by Richardson & van Wilgen (2004), including (A) main geographical barriers; (B) local environmental barriers; (C) reproductive barriers; (D) dispersal barriers; (E) environmental barriers in disturbed habitats; and (F) environmental barriers in undisturbed habitats. Very few species overcome all the barriers, but those that do so can have a severe impact. For a species to become invasive in a new

Figure 4 Predicted worldwide distribution of *Ceratitis capitata* using a genetic algorithm for rule-set prediction (GARP) and a technique based on principal components analysis (PCA). White, predicted absence; light grey, low confidence in predicted presence; dark grey, higher confidence in predicted presence; black, high confidence in predicted presence. Dotted squares indicate the native range of *C. capitata*; open squares, non-native populations of *C. capitata*; triangles, indicate non-native temporary establishment of *C. capitata*. First inset, predicted distribution of *C. capitata* in southern Europe and the Mediterranean; second inset, its distribution in the southern USA.

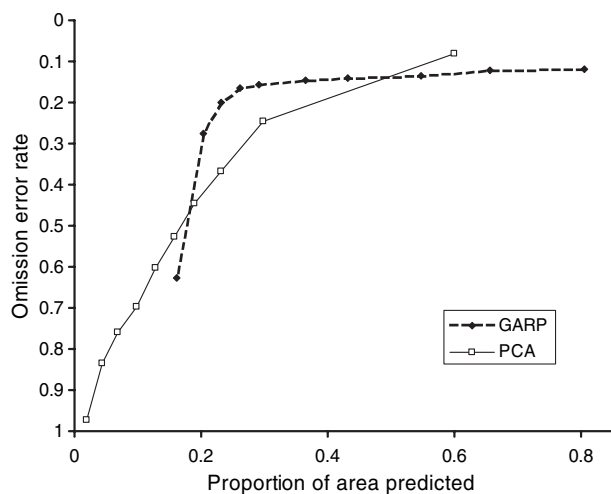


Figure 6 Comparison of accumulation of predictive ability vs. proportion of area (worldwide) predicted present in genetic algorithm for rule-set prediction (GARP) and principal components analysis (PCA) models.

region, it needs to be introduced to that region (barrier A). It needs to survive in the new region (barrier B) and reproduce (barrier C). Next, the population needs to increase sufficiently to allow dispersal to new areas (barrier D). Some species, particularly plants, persist only in disturbed habitats (barrier E), but some are able to invade undisturbed habitats (barrier F) to become transformer species. An important factor to consider, especially with fruit flies, is competition with indigenous species or with other introduced species (Duyck *et al.*, 2004). Competition could be considered as part of barriers C and D.

In the context of the current study, we are able to examine only the suitability of the climate of the new region (barrier B). To assess invasion risk for a particular region of the world, all the other barriers have to be assessed (Thuiller *et al.*, 2005). The maps presented here cannot be interpreted as maps of invasion risk or likelihood of establishment for these species. Indeed, a region that has an apparently suitable climate for the species is likely to be more vulnerable than one where the climate is unsuitable. However, we do not know whether individuals of the species will be introduced to that region. We also do not know whether individuals that are introduced will survive the local conditions for long enough to breed successfully, or whether the conditions will allow for breeding.

Propagule pressure (also known as introduction effort) has been identified as an important factor in explaining establishment success of introduced organisms (Lockwood *et al.*, 2005; Thuiller *et al.*, 2005, 2006; Colautti *et al.*, 2006). Propagule pressure is a measure of the number of individuals released into a region where they are not native. It is a combined measure that includes propagule size; the number of individuals involved in a single release event; and propagule number, which is the number of discrete release events (Lockwood *et al.*, 2005). Propagule pressure increases as the number of

releases and/or the number of individuals released increases. A number of studies, reviewed by Lockwood *et al.* (2005), have found that propagule pressure explained significant variation in establishment success of organisms. A recent meta-analysis by Colautti *et al.* (2006) found that invasive species that established tended to occupy similar habitats to those occupied in the native range. They also found that established species were introduced more often and/or in greater numbers (higher propagule pressure) than a contrast group of species (mostly introduced species that failed to establish). Propagule pressure has been shown to be important for the establishment of insects that are used as biocontrol agents for plants (Memmott *et al.*, 2005). Thuiller *et al.* (2005) produced bioclimatic niche models for 96 plant taxa that are endemic to South Africa but invasive elsewhere, and projected these globally. They produced maps of cumulative probabilities of climate suitability for these species. They found that these probabilities were significantly correlated with the number of recorded invasive species of South African origin in natural areas. This indicates that climate plays an important role in determining invasion potential, but is not the only factor. When they accounted for propagule pressure (using trade and tourism data as a surrogate), the explanatory power of climate suitability as an index of invasibility increased significantly. This work suggests an important role for climate suitability and propagule pressure in invasion success.

Quarantine procedures are designed specifically to reduce propagule pressure of undesirable species. Quarantine procedures are already in place in a number of countries that import fresh products from the regions where *C. capitata* is known to occur, with the intention of preventing further introductions of this species. Most procedures intended for *C. capitata* will also be effective for other fruit fly species with a similar host range, including *C. rosa*. The same applies to fruit disinfestation methodologies such as fumigation, cold or hot treatments, controlled atmosphere, radiation or fruit dipping (Armstrong & Couey, 1989; Rigney, 1989), although specific modalities for some of them might differ among taxa.

A question of particular interest is why *C. capitata* has become invasive throughout the world, whereas *C. rosa* has not, despite both species having broadly similar native distributions. Several differences in morphological, physiological or behavioural adaptive traits may be the cause of this. Although these have been studied in detail for *C. capitata* (reviewed by Malacrida *et al.*, 2006), there is scant information for other potential pest species, including *C. rosa*, in order to allow comparative analysis. Recently it has been stated that genetic architecture, which might influence a species' ability to respond to natural selection, could play an important role in invasion success (Lee, 2002). To answer this question fully, one would need to compare the biology of both species in the context of the system of barriers outlined above. However, the fact that *C. rosa* did invade some Indian Ocean islands, and that it was able to dominate over *C. capitata* in those particular regions, may be a cause for concern.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

Table S1 Records for *Ceratitis capitata* from outside of sub-Saharan Africa.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2007.01769.x>

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BIOSKETCH

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